

THE IMPLICATIONS OF LUNG-REGULATED BUOYANCY CONTROL FOR DIVE DEPTH AND DURATION

GRAEME C. HAYS,^{1,4} JULIAN D. METCALFE,² AND ANTHONY W. WALNE³

¹*School of Biological Sciences, University of Wales Swansea, Singleton Park, Swansea SA2 8PP, UK*

²*The Centre for Environment, Fisheries and Aquaculture Science, Lowestoft Laboratory, Lowestoft NR33 0HT, UK*

³*Sir Alister Hardy Foundation for Ocean Science, Citadel Hill, Plymouth, UK*

Abstract. Among air-breathing divers, control of buoyancy through lung volume regulation may be most highly developed in marine turtles. In short, the turtle lung may serve a dual role as both an oxygen store and in buoyancy control. A simple model is developed to show that, for turtles diving up to the maximum depth at which they can still use their lungs to attain neutral buoyancy, the total oxygen store will increase greatly with dive depth, and hence a corresponding increase in dive duration is predicted. Time–depth recorders attached to free-living green turtles (*Chelonia mydas*) at Ascension Island confirmed a marked increase in dive duration with depth, with the gradient of this relationship being >10 times that seen in diving birds and mammals. Consistent with the prediction that the lungs serve a dual role, we found that, when lead weights were added to some turtles to increase their specific gravity, the mean depth of dives decreased, but for dives to the same depth, weighted animals dived for longer. The depth distribution of green turtles seems to be generally constrained by the maximum depth at which they can still attain close to neutral buoyancy.

Key words: *Ascension Island; bird; buoyancy control; Chelonia mydas; depth selection; diving; green turtle; mammal; penguin; pinniped; seal.*

INTRODUCTION

For marine vertebrates there is a broad dichotomy between those that may stay submerged permanently (fish) vs. those that must regularly surface to breathe (mammals, birds, and reptiles) and this requirement to breathe in some groups may impose a conflict between achieving maximal oxygen stores for a dive and minimizing the cost of swimming. In short, maximizing the oxygen store through full inspiration at the surface will make it harder for a diver to descend. Consequently, some accomplished deep-diving mammals exhale prior to submergence, which reduces their oxygen stores, so that the dive is sustained mainly with oxygen stores in their blood and tissues (Butler and Jones 1997). However, even with exhalation prior to submergence, the volume of gas in the lungs may still be critical in determining a diving mammal's overall density and often, at some point during the descent, there is a switch from positive to negative buoyancy due to gas compression with depth. For example, for some diving seals, whales, and porpoises, the start of the descent tends to be characterized by active fin stroking as the animals work to overcome initial positive buoyancy and then, once the animal is deeper and has attained negative buoyancy through lung compression, the descent is maintained through long periods of pas-

sive gliding (Skrovan et al. 1999, Williams et al. 2000, Davis et al. 2001, Williams 2001). This passive gliding is thought to help reduce the metabolic rate during the dive, allowing an extension of the aerobic dive limit. Passive gliding during descent is also seen on deep dives by penguins (Sato et al. 2002), but, on shallow dives, birds are often positively buoyant even during the bottom phase of dives due to the large amount of air trapped in the plumage, and so they rapidly bob up to the surface if they stop swimming (Wilson et al. 1992). Penguins may modify their inspired lung volume depending on their dive depth in order to improve the efficiency of descending and ascending (Sato et al. 2002). Yet, among divers, the role of the lungs in buoyancy regulation may be most developed in hard-shelled marine turtles, i.e., all species except the leatherback turtle, *Dermochelys coriacea*. Yet, comparative studies of diving in air-breathing vertebrates have tended to focus on marine mammals and birds (e.g., Boyd 1997, Butler and Jones 1997, Schreer et al. 2001) while information on marine turtles is far more scant. Hard-shelled turtles tend to be relatively shallow divers, rarely diving deeper than 25 m (e.g., van Dam and Diez 1996, Hochscheid et al. 1999, Houghton et al. 2002). It has been known for many years that hard-shelled marine turtles may modify their inspired lung volume to adjust their level of buoyancy during dives (Milsom and Johansen 1975) and this lung-regulated buoyancy may have fundamental implications for the available oxygen store on dives to different depths. In order to attain close to neutral buoyancy on the bottom phase,

Manuscript received 14 April 2003; revised 11 July 2003; accepted 31 July 2003; final version received 21 August 2003.
Corresponding Editor: T. D. Williams.

⁴ E-mail: g.hays@swan.ac.uk

a larger presubmergence inspiration is required on deeper dives, i.e., the oxygen stores will increase on deeper dives. When diving aerobically the dive duration is constrained by the oxygen stores and the metabolic rate (Minamikawa et al. 2000) and so, all other things being equal, we would predict increasing dive duration on deeper dives in hard-shelled turtles. Here we develop a simple model to show how the oxygen stores may vary with dive depth and buoyancy in marine turtles and hence we predict how dive duration will vary with dive depth. We then test the predictions of the model by using time–depth recorders to record the free-living diving behavior of green turtles (*Chelonia mydas*). Furthermore, by experimentally manipulating the specific gravity of some individuals, by the addition of lead weights, we examine whether the turtles both adjust their lung volume and their diving depth in line with model predictions.

MATERIALS AND METHODS

Between 21 March and 26 March 2002, we attached time–depth recorders (TDRs) to 25 female green turtles that had just completed nesting on Long Beach, Ascension Island, South Atlantic (7°57' S, 14°22' W). TDRs were attached with quick-setting epoxy to either the head or the carapace of the turtles as described previously (Hays et al. 2000, 2002). In addition, for some turtles, a lead weight was also attached to the carapace, again with epoxy. Two types of TDR were used (both manufactured by LOTEK Marine Technologies, St. John's, Newfoundland): (a) LTD_1200, which recorded depth every 5 s with resolution of 4 cm, and (b) LTD_1100, which recorded depth every 52 s with resolution of 30 cm. Long Beach was patrolled subsequently to relocate instrumented turtles when they emerged to lay their subsequent clutch and at this time the equipment was removed and the TDR data downloaded to a personal computer. Dive data were analyzed using dedicated dive analysis software (MultiTrace, Jensen Software Systems, Laboe, Germany). To extract dive parameters for each dive, dives were defined as having a maximum depth of ≥ 5 m, with the start and end of the dive occurring when the vertical descent/ascent rate exceeded 0.3 m/s. The start and end of the bottom phase was defined by a threshold vertical speed of 0.02 m/s. Visual analysis of individual dive profiles confirmed that the software successfully captured dives. For each dive the duration, maximum depth, and the mean depth of bottom phase were determined.

In many regions, turtles have been reported to spend a large proportion of their time resting on the seabed (e.g., van Dam and Diez 1996, Hays et al. 2000) and presumably while on the seafloor such turtles are only slightly negatively buoyant so that they (i) do not have to work against positive buoyancy during the bottom phase of these dives and (ii) upon termination of the dive they can ascend with little difficulty back to the surface to breathe. During these benthic resting dives

there is very little variation in depth during the bottom phase, giving rise to a characteristic U-shaped profile. These resting dives serve as a useful dive type for examining links between dive depth and duration, since there is presumably little between-dive variation in metabolic rate, and hence the confounding effects of metabolic rate on dive duration are minimized. We therefore focused our analysis on U-dives.

RESULTS

Conceptual framework for oxygen stores and dive depth

Assuming no tissue resistance, as a turtle dives, the lungs will be compressed in accordance with Boyle's Law, so that as the depth increases, the volume of lungs will decrease. After inhaling at the surface, turtles are positively buoyant and are therefore able to rest passively at the surface. However, as they descend, they will lose buoyancy as the lungs are compressed, until, at a certain depth, they become neutrally buoyant. The maximum depth for neutral buoyancy (MDNB) is therefore defined as the depth at which a turtle attains neutral buoyancy after diving with fully inflated lungs. If a turtle is to attain neutral buoyancy at a shallower depth, it follows that the turtle must only partly inflate its lungs before submerging and so the O_2 store will be less. Given the values for the lung volume, the O_2 content of the lung, and blood and tissue O_2 store, it is possible to calculate the O_2 store for a dive. Since MDNB has not been measured for marine turtles, in order to assess the potential importance of this parameter we constructed a model in which a range of values for MDNB were assumed in combination with a range of dive depths.

If V_m = the maximum lung volume (L/kg body mass) following full inspiration at the surface, O_1 = the oxygen content (proportion) of the lung immediately following inspiration, and O_{bm} = the oxygen content (L O_2 /kg body mass) of the blood and muscles at the start of a dive, then the maximum oxygen store (i.e., following full inspiration) is given by

$$(V_m \times O_1) + O_{bm}$$

Similarly, if the turtle is to attain neutral buoyancy at the maximum depth on a U-shaped dive, we can readily calculate how the oxygen store will vary as a function of the value for MDNB and the depth of that U-dive. Since water pressure increases by 1 atmosphere ($\approx 1 \times 10^5$ Pa) for every 10 m of depth, we can define the water pressure (p , in atmospheres) at any depth (d , in meters) as

$$p = (d/10) + 1.$$

Following Boyle's Law, since $p_1 \times v_1 = p_2 \times v_2$ (where p_1 and p_2 are the pressures and v_1 and v_2 are the lung volumes, at depths 1 and 2 respectively), then if V_{LNB} = the lung volume at the depth where neutral

buoyancy is attained, at MDNB (maximum depth of neutral buoyancy in meters),

$$V_{\text{LNB}} = V_m / [(MDNB/10) + 1]$$

then the lung volume following inspiration at the surface (V_{LS}) is given by

$$V_{\text{LS}} = V_{\text{LNB}} \times p.$$

The total oxygen store (in L O₂/kg body mass) for the dive is then given by total oxygen store = ($V_{\text{LS}} \times O_1$) + O_{bm} .

Previous studies with hard-shelled marine turtles have estimated that the O₂ content of the lungs (O_1) at the start of a dive is 0.174 (Berkson 1966); the oxygen content of the blood and muscles (O_{bm}) is 0.0067 L O₂/kg body mass (Lutz and Bentley 1985); while the maximum lung capacity (V_m) averages 0.094 L/kg body mass for loggerhead turtles (*Caretta caretta*; Berkson 1966, Lutz and Bentley 1985), while a maximum value of 0.12 L/kg body mass being estimated for green turtles (Tenney et al. 1974). The scaling of V_m with turtle size is unknown. Using these literature values for the various oxygen stores, Fig. 1 shows how the total oxygen stores for dives to different depths will vary assuming different values for MDNB and assuming that turtles attain neutral buoyancy during the bottom phase. From Fig. 1, a few key points are evident. First it can be seen that the available oxygen store plateaus once the depth of the dive is deeper than MDNB. For dives shallower than this depth, the oxygen store will be less than this maximal value. Most importantly, when diving to shallower than MDNB, the total oxygen store varies quite dramatically with dive depth. For example, when MDNB \geq 16 m, the total oxygen store increases by \sim 40% for dives to 15 m compared to 5 m. However, it is important to note that the oxygen store is not simply a function of the dive depth, but also of MDNB.

Dive types and predictions of dive depth and duration

We can make several predictions about how the duration of U-dives should vary as a function of depth and how attaching weights to green turtles might affect both the depth and duration of these dives.

Prediction 1. Dive depth vs. duration.—Regardless of MDNB, at depths shallower than MDNB the oxygen stores increase markedly with depth. For example, assuming $V_m = 0.094$ L/kg body mass then if MDNB is 12 m, the total oxygen stores increase from 0.017 L O₂/kg body mass at 4 m to 0.023 L O₂/kg body mass at 10 m; while if MDNB is 20 m, the total oxygen store increases from 0.014 L O₂/kg body mass at 4 m to 0.023 L O₂/kg body mass at 20 m. If the metabolic rate is similar on U-dives to different depths we would likewise expect a similar increase of dive duration with depth.

Prediction 2. Weighted vs. unweighted animals.—If turtles routinely dive well within the depth range over

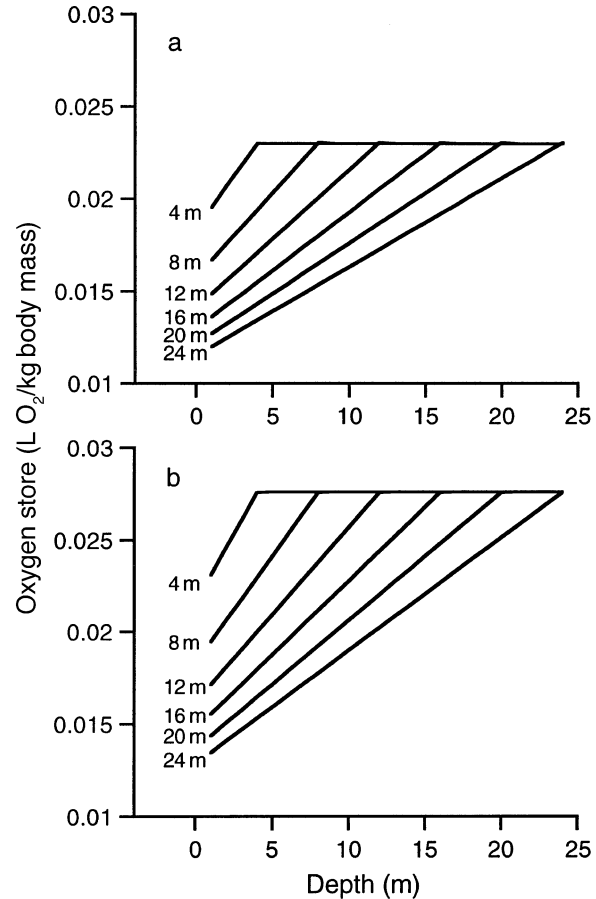


FIG. 1. For green turtles, the model predictions for the mass-specific O₂ store for dives as a function of MDNB and the depth for that particular dive. Note that MDNB has not been measured for marine turtles and so to examine the importance of this parameter a range of assumed values for MDNB were incorporated into the model. Values for MDNB are shown on each plot. Panel (a) assumes a maximum lung capacity (V_m) of 0.094 L/kg while (b) assumes that $V_m = 0.12$ L/kg. When the dive depth equals or exceeds MDNB (i.e., the plateau on the graph), then the O₂ store is maximal, i.e., the turtle will begin that dive with fully inflated lungs and so the O₂ store cannot increase further.

which they can control their buoyancy, then weighted turtles might simply dive to the same depth as unweighted animals, but increase their inspired air volume to attain the same level of buoyancy during the bottom phase. Under this scenario, for dives to the same depth, the oxygen store would be greater in weighted vs. unweighted animals and so we would expect the dive duration to be longer for the weighted animals. Alternatively, if turtles routinely dive close to the maximum depth at which they can attain close to neutral buoyancy (i.e., that depth dictated by the lung compression following a full inspiration at the surface), then they will not be able to increase their inspired lung volume any further following the addition of weights. Consequently, if weighted animals dived to

TABLE 1. The curve carapace length (CCL), interesting interval, size of weight attached, number of U-dives recorded, mean depth during the bottom phase, and mean dive duration for each turtle.

Turtle no.	CCL (cm)	Interesting interval (d)	Weight attached (kg)	Number of U-dives	Mean depth m (± 1 SD)	Mean duration min (± 1 SD)
1†	108	12	NA	232	14.4 (3.6)	30.8 (8.2)
2†	121	11	NA	220	12.1 (2.7)	27.5 (7.5)
3†	115.5	13	NA	318	17.5 (2.5)	36.4 (7.1)
4†	107	11	NA	225	14.9 (2.9)	30.1 (9.2)
5‡	107.5	11	NA	200	15.1 (2.7)	35.1 (7.8)
6‡	107.5	11	NA	182	17.1 (1.9)	39.7 (8.3)
7†	122.5	14	2.0	236	13.5 (3.2)	38.9 (9.3)
8†	110	12	1.9	285	12.8 (1.6)	34.6 (8.3)
9†	114.5	11	2.0	260	13.7 (2.7)	37.6 (13.2)
10†	103.5	11	1.7	289	13.3 (3.3)	28.7 (6.7)
11†	115.5	11	1.8	254	14.0 (5.2)	30.6 (11.1)

† LTD-1200 model time–depth recorder.

‡ LTD-1100 model time–depth recorder.

the same depth as unweighted individuals, they would be more negatively buoyant during the bottom phase, their oxygen stores would be the same, and so their dive duration would not be longer. However, if maintenance of appropriate buoyancy during the bottom phase of dives is important, then under this scenario we would predict that weighted animals would be forced to rest at shallower depths so that they could still attain the same level of buoyancy on the seafloor as unweighted animals.

Empirical observations

Eleven TDRs were recovered from turtles returning to re-nest after intervals of between 11 and 14 d (Table 1), with five of these 11 turtles being fitted with weights. All turtles performed U-dives to the seafloor, often in long bouts, indicative of benthic resting (Fig. 2). The number of U-dives recorded for each individ-

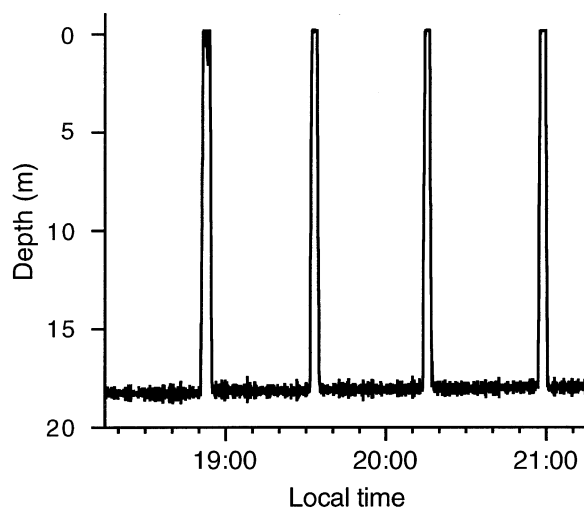


FIG. 2. An example of a series of U-dives performed by an interesting turtle at Ascension Island. The plot shows linear interpolation between individual depth readings recorded every 5 s.

ual, their mean depth and duration and the size of weights attached is shown in Table 1. While there was a general tendency for dive duration to increase with dive depth in all turtles, there were differences in the exact nature of this relationship between individuals and in all cases depth only explained a minority of the variation in dive duration (Fig. 3). To provide a general description of the nature of the duration vs. depth relationship we pooled all the dives for unweighted turtles. The resulting least-squares-fit regression of duration vs. depth had a gradient of 1.65 (Fig. 4). While dive duration increases with depth in a range of air-breathing divers, this gradient for green turtles is an order of magnitude higher than that recorded in a variety of diving birds and pinnipeds (Fig. 5).

While the duration of U-dives tended to increase with dive depth in both weighted and unweighted animals, for dives to any particularly depth, the corresponding mean dive duration was longer in the weighted animals for dives up to 17 m (paired *t* test, $P < 0.001$; Fig. 6). The exception to this pattern was for the deeper dives (>17 m) where there was no clear difference in the dive durations between the two groups of animals.

The mean depth of U-dives was significantly shallower for weighted (mean = 13.4 m, 1 SD = 3.4, $n = 1324$ dives) vs. unweighted animals (mean = 15.3 m, 1 SD = 3.3, $n = 1375$ dives ($t_{2609} = 14.1$, $P < 0.001$). There was also a clear difference in the modal depth of weighted vs. unweighted animals (12.5 m and 17.5 m respectively; Fig. 7). This difference in the depth of U-dives between weighted and unweighted animals grew larger as the interesting interval progressed. For example, during days 1 and 2 of the interesting interval, the mean depth of U-dives for weighted animals was 0.7 m shallower than for unweighted animals, but by days 7 and 8 this difference had grown to 3.0 m (Fig. 8). Hence the difference between the frequency distributions for the depth of U-dives for weighted and unweighted animals became more pronounced by the second half of the interesting interval (Fig. 7c and d).

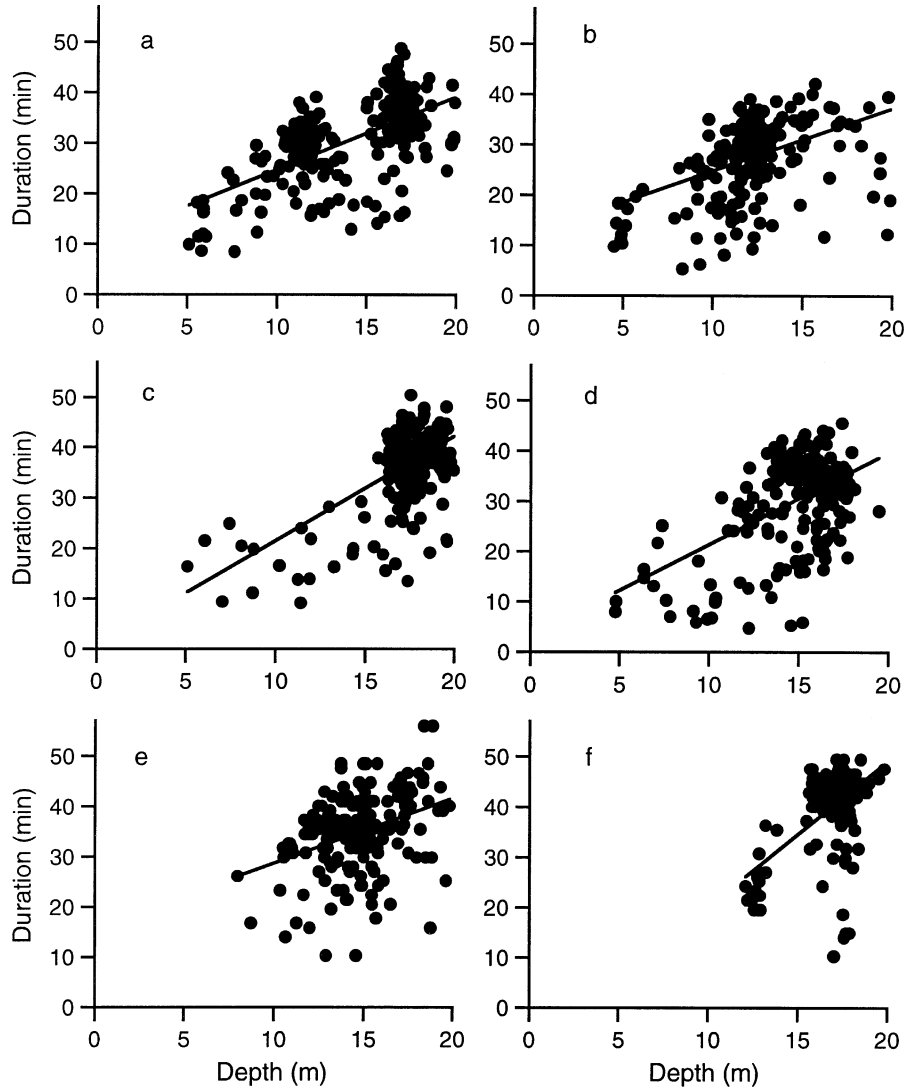


FIG. 3. For six unweighted turtles, the relationships between dive duration and depth for U-dives to between 5 m and 20 m. Panels (a)–(f) represent turtles 1–6, respectively. The increase in duration with depth is significant ($P < 0.001$) in all cases with the gradient of these relationships being 1.45, 1.26, 2.08, 1.83, 1.30, and 2.91 for turtles 1–6, respectively, and the r^2 for the relationships being 0.38, 0.21, 0.36, 0.25, 0.13, and 0.31, respectively.

DISCUSSION

Our theoretical arguments and empirical evidence highlight the importance of lung-regulated buoyancy during dives by green turtles. In short, while mammals and birds may make use of their lungs as an oxygen store to a greater or lesser extent depending on the species, in turtles the lungs seem to provide a dual role of both an important oxygen store and in buoyancy control, and dive depths are routinely constrained within the range over which buoyancy can be regulated. Our empirical evidence suggests that, in turtles, the implications of gas compression with depth lead to modifications in the inspired air volume prior to the dive commencing, i.e., the final pre-dive inspiration is modified in anticipation of the dive to come. This an-

ticipation is presumably fairly easy to develop in turtles, because there are often discrete bouts of dives to the same depth, so that the target depth is probably known exactly. As a consequence of this modification of the inspired air volume, the total oxygen store for a dive, and hence dive duration, increases rapidly with depth. While the total oxygen store for green turtles is predicted to increase maximally by about 1.4 times between dives to 5 m and 15 m, the actual mean dive duration increased about 2 times over this depth range (regression equation to Fig. 4). In other words, the increase in dive duration with depth was more than might be expected from the model. One possibility is that the metabolic rate may be lower for deeper dives or alternatively turtles more closely approach their aer-

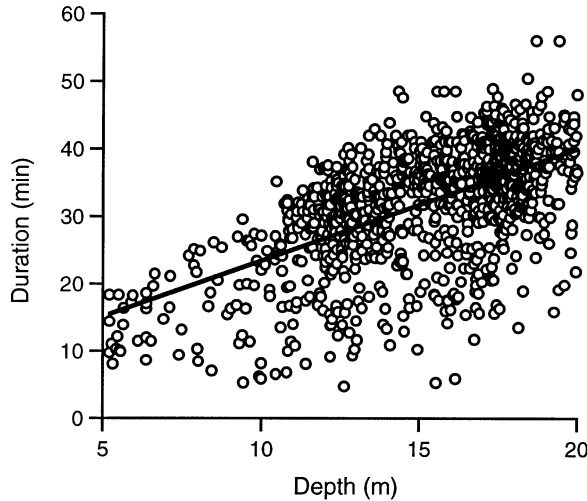


FIG. 4. The relationship between dive duration and maximum depth for U-dives shallower than 20 m. Duration (min) = 6.94 + 1.65(depth) (m); $F_{1,1349} = 780$, $r^2 = 0.37$, $P < 0.001$.

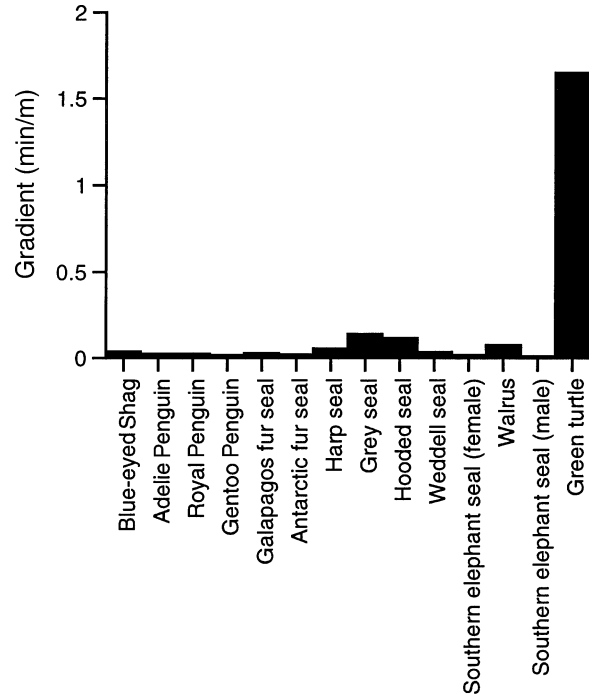


FIG. 5. For a number of air-breathing divers, the gradient of the relationship between duration and maximum depth of U-dives. Values for diving birds and pinnipeds are from Schreer et al. (2001). The value for green turtles is from Fig. 4.

obic dive limit on deeper dives. However, there was not a simple linear increase in dive duration across the full depth range, rather, for the unweighted animals, there was a similar mean dive duration for dives to between 17 and 20 m. This suggests that 17 m was close to the MDNB for unweighted animals, since deeper than MDNB we predict that the oxygen stores (and hence dive duration) cannot increase further. The modal resting depth was also 17 m, suggesting that the unweighted animals often chose to rest near their MDNB. In reality, the turtles most probably are very slightly negatively buoyant when sitting on the seafloor, so that they do not float upwards during these benthic dives. Being a volcanic island, there is only a narrow band of shallow water surrounding Ascension Island and so turtles were certainly resting on the seabed within only a few kilometers of the shore. Furthermore, the water depth around Ascension Island changes from a few meters to many hundreds of meters over a very short horizontal scale (<1 km) and so dive depth is not constrained by the availability of different depths.

Superimposed on the general pattern for deeper dives to be longer in green turtles, it was clear that there was considerable individual variation in this relationship and, in all cases, depth only explained a minority of the variation in dive duration. The reasons for both these inter- and intraindividual variations in dive duration are unknown and merit further examination. Regardless of the causes of this variation, it was clear that the gradient of the relationship between dive duration vs. depth was much greater in green turtles compared to marine mammals and birds. This difference may partly reflect the increasing oxygen store on deeper dives in green turtles. However, much of this difference will reflect the fact that green turtles are ectothermic

while the other two groups are endothermic. This ectotherm–endotherm dichotomy means that the weight-specific metabolic rate of green turtles is around an order of magnitude lower than mammals and birds and consequently, all other things being equal, the gradient

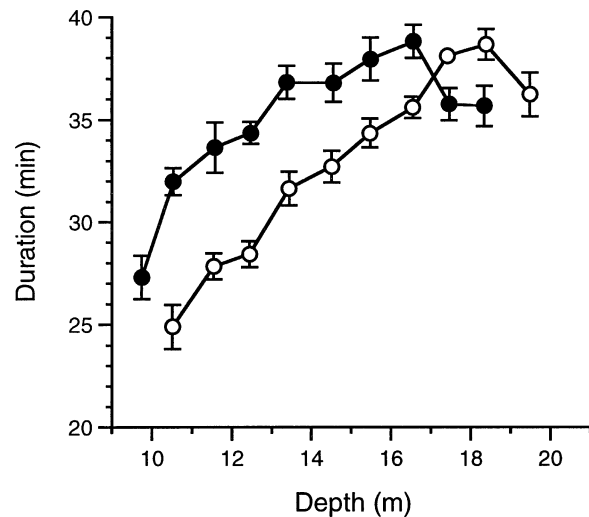


FIG. 6. The relationship between the depth and duration of U-dives. Filled circles represent weighted animals; open circles represent unweighted animals. Mean values for duration were calculated for 1-m depth increments, including only those depth increments where there were at least 50 dives recorded. Error bars represent ± 1 SE.

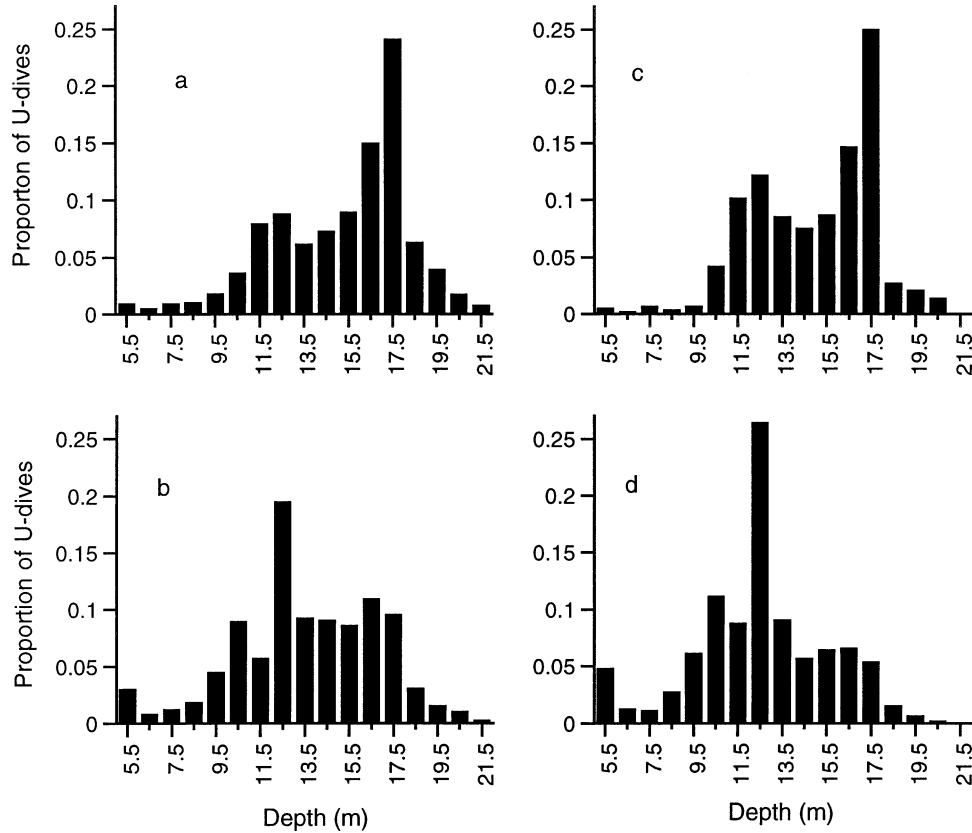


FIG. 7. Frequency histograms showing the proportion of U-dives to different depths: (a) unweighted and (b) weighted individuals, including data from throughout the interesting interval; (c) unweighted and (d) weighted individuals, including data from days 6, 7, 8, 9, and 10 of the interesting interval.

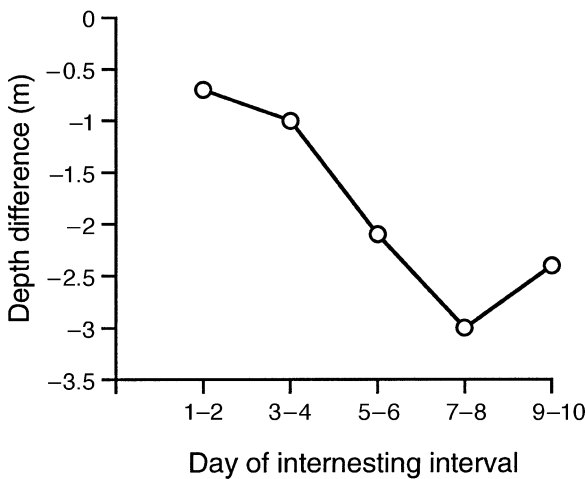


FIG. 8. The difference between the mean depth of U-dives for weighted and unweighted animals during the course of the interesting interval. Minus values denote the mean depth of weighted individuals was the shallower.

of the duration vs. depth relationship will be an order magnitude higher in green turtles compared to the other groups.

Theoretical considerations clearly show that MDNB is a vital parameter for assessing the oxygen stores during turtle diving. Experimental manipulation of the specific gravity of turtles can be used to provide further evidence for the value of MDNB. There are a number of ways in which the implications of individual differences in animal density on diving performance can be examined. First, diving behavior can be compared between different times of year if there are marked seasonal changes in body composition. This approach is particularly suitable for marine mammals, where seasonal changes in fat levels, and hence buoyancy, can be huge (Crocker et al. 1997, Webb et al. 1998, Beck et al. 2000). Second, the specific density of individuals can be artificially altered through the addition of weights and floats. In some cases, weights may be jettisoned at predetermined intervals so that for each individual there is a set of observations for the weighted and unweighted condition (e.g., Minamikawa et al. 2000). Slightly less elegant is the approach we adopted in which simply one group of individuals is weighted and another group is left unweighted (e.g., Webb et al.

1998). A potential problem with this approach is that natural individual variation in dive depths and durations might mask the effects of the experimentally induced changes in animal density. In short, we might potentially have made a type 2 error, failing to identify a real effect of the weights. For two loggerhead turtles in Japan (mean mass 100.5 kg), the lead weights attached were 1.3% of the mass of the turtles and produced very clear effects on the diving behavior (Minamikawa et al. 2000). Using a previously published relationship between the curve carapace length (CCL) and the mass of green turtles at Ascension Island (mass in kg = $4.585 \times \text{CCL [in cm]} - 349.22$) (Hays et al. 2000), we can predict that the weights we attached equaled 1.1% of the body mass of the turtles (mean mass of weighted turtles = 170 kg). Hence we would qualitatively predict that the added weights would be sufficiently large to affect the diving behavior of the turtles at Ascension Island.

When diving to the same depth as unweighted animals, weighted animals would need to increase their inspired lung volume in order to attain the same level of buoyancy and the resulting increased oxygen store would be expected to prolong the duration of dives. Hence an increase in dive duration between weighted vs. unweighted animals diving to the same depth, indicates that weighted animals are still diving to a depth where they are able to control their buoyancy to some extent, i.e., shallower than MDNB. We found that, for dives to between 9 and 17 m, dive duration was longer in the weighted animals in accord with these arguments. However, for slightly deeper dives (17–19 m), the dive duration of weighted vs. unweighted animals was similar, suggesting again that at these depths both groups of animals were diving after maximal inspiration.

We can make some simple calculations to estimate the extra dive duration that might be expected in weighted animals. The mean weight (in air) of lead that we attached was 1.88 kg. Since lead has a density of 11.4 g/cm^3 while sea water has a density of 1.027 g/cm^3 , a 1.88 kg lead weight would weigh 1.71 kg in sea water. If a turtle had to support an extra 1.71 kg underwater, this would require an extra 1.71 L of gas in the lungs, which, if the turtle was resting at 12 m, would equate to an extra inspired air volume of $2.2 \times 1.71 = 3.76 \text{ L}$ of air. Assuming that the oxygen content of the lungs was 17.4% (Berkson 1966), this extra 3.76 L of air would equate to 0.65 L O_2 . Prange and Jackson (1976) recorded the metabolic rate for adult green turtles resting on land while nesting as $0.024 \text{ L O}_2\text{-kg}^{-1}\text{-h}^{-1}$. If we assume that the turtles resting underwater had this metabolic rate, then a 170-kg turtle (the predicted mean mass of the weighted turtles) would have a metabolic rate of $4.08 \text{ L O}_2/\text{h}$. Hence the extra 0.65 L of oxygen would sustain an extra 9.5 min of diving. Such calculations clearly need to be treated with a large degree of caution since they make a number of assumptions, but they still serve to illustrate how,

when diving shallower than the MDNB, weighted turtles would be expected to increase their dive duration by a few minutes which is essentially what they were observed to do.

Our conclusion that the MDNB for green turtles at Ascension Island is around 17 m, is broadly consistent with the conclusion that, for loggerhead turtles in Japan, MDNB is around 14 m. There is the suggestion that MDNB might increase with body size in turtles, since for small hawksbill turtles (*Eretmochelys imbricata*) in a cliff wall habitat in the Caribbean, resting dives were typically shallower than 10 m (van Dam and Diez 1996). However, quantitative exploration of this hypothesis will require such behavioral observations to be extended with measurements of lung volumes and gas free weights in water (following the procedures used previously on sea snakes [Graham et al. 1975, 1987]) for turtles of a range of sizes. Potentially, the resting depth for turtles at Ascension might not be related to the MDNB but instead might simply be a consequence of the availability of suitable benthic environments in which to rest. However the fact that weight manipulation altered the distribution of resting depths in such a predictable manner suggests that the MDNB does indeed dictate why green turtles at Ascension Island rarely rest deeper than 20 m.

The length of time that turtles take to adjust to added weights seems to be variable. For loggerhead turtles during the internesting interval in Japan, the dive depth was adjusted relatively quickly (<30 min) after weights detached (Minamikawa et al. 2000), while Milsom and Johansen (1975) reported that compensation to added weights was completed within 24 h. For green turtles at Ascension Island, the difference in depth of diving between weighted vs. unweighted animals was most pronounced during the second half of the internesting period, suggesting again that full adjustment of behavior to the added weights may have taken some time.

In conclusion, while hard-shelled marine turtles sometimes dive to a few tens of meters, or even beyond 100 m very occasionally (Lutcavage and Lutz 1997), our evidence suggests that where a range of potential depths are available, green turtles usually select their resting depth within the range over which they can use their lungs to achieve close to neutral buoyancy. With this tight interaction between buoyancy control and depth of diving, green turtles appear to differ fundamentally in their diving behavior compared to marine mammals and birds.

ACKNOWLEDGMENTS

We thank the Administrator for Ascension Island, H. H. Geoffrey Fairhurst, for his support during our stay on Ascension Island. This work was supported by a grant to G. C. Hays from the Natural Environmental Research Council of the UK (NERC).

LITERATURE CITED

Beck, C. A., W. D. Bowen, and S. J. Iverson. 2000. Seasonal changes in buoyancy and diving behaviour of adult grey seals. *Journal of Experimental Biology* **203**:2323–2330.

- Berkson, H. 1966. Physiological adjustments to prolonged diving in the Pacific green turtle (*Chelonia mydas agassizii*). *Comparative Biochemistry and Physiology* **18**:101–119.
- Boyd, I. L. 1997. The behavioural and physiological ecology of diving. *Trends in Ecology and Evolution* **12**:213–217.
- Butler, P. J., and D. R. Jones. 1997. Physiology of diving of birds and mammals. *Physiological Reviews* **77**:837–899.
- Crocker, D. E., B. J. Le Boeuf, and D. P. Costa. 1997. Drift diving in female northern elephant seals: implications for food processing. *Canadian Journal of Zoology* **75**:27–39.
- Davis, R. W., L. A. Fuiman, T. M. Williams, and B. J. Le Boeuf. 2001. Three-dimensional movements and swimming activity of a northern elephant seal. *Comparative Biochemistry and Physiology A* **129**:759–770.
- Graham, J. B., J. H. Gee, J. Motta, and I. Rubinoff. 1987. Subsurface buoyancy regulation by the sea snake *Pelamis platurus*. *Physiological Zoology* **60**:252–261.
- Graham, J. B., J. H. Gee, and F. Robison. 1975. Hydrostatic and gas exchange functions of the lung of the sea snake *Pelamis platurus*. *Comparative Biochemistry and Physiology* **50A**:447–482.
- Hays, G. C., C. R. Adams, A. C. Broderick, B. J. Godley, D. J. Lucas, J. D. Metcalfe, and A. A. Prior. 2000. The diving behaviour of green turtles at Ascension Island. *Animal Behaviour* **59**:577–586.
- Hays, G. C., F. Glen, A. C. Broderick, B. J. Godley, and J. D. Metcalfe. 2002. Behavioural plasticity in a large marine herbivore: contrasting patterns of depth utilisation between two green turtle (*Chelonia mydas*) populations. *Marine Biology* **141**:985–990.
- Hochscheid, S., B. J. Godley, A. C. Broderick, and R. P. Wilson. 1999. Reptilian diving: highly variable dive patterns in the green turtle, *Chelonia mydas*. *Marine Ecology Progress Series* **185**:101–112.
- Houghton, J. D. R., A. Broderick, B. Godley, J. D. Metcalfe, and G. C. Hays. 2002. Diving behaviour during the interesting interval for loggerhead turtles *Caretta caretta* nesting in Cyprus. *Marine Ecology Progress Series* **227**:63–70.
- Lutcavage, M. E., and P. L. Lutz. 1997. Diving physiology. Pages 277–296 in P. L. Lutz and J. A. Musick, editors. *The biology of sea turtles*. CRC Press, Boca Raton, Florida, USA.
- Lutz, P. L., and T. B. Bentley. 1985. Respiratory physiology of diving in the sea turtle. *Copeia* **1985**:671–679.
- Milsom, W. K., and K. Johansen. 1975. The effect of buoyancy induced lung volume changes on respiratory frequency in a Chelonian (*Caretta caretta*). *Journal of Comparative Physiology* **98**:157–160.
- Minamikawa, S., Y. Naito, K. Sato, Y. Matsuzawa, T. Bando, and W. Sakamoto. 2000. Maintenance of neutral buoyancy by depth selection in the loggerhead turtle *Caretta caretta*. *Journal of Experimental Biology* **203**:2967–2975.
- Prange, H. D., and D. C. Jackson. 1976. Ventilation, gas exchange and metabolic scaling of a sea turtle. *Respiration Physiology* **27**:369–377.
- Sato, K., Y. Naito, A. Kato, Y. Niizuma, Y. Watanuki, J. B. Charrassin, C. A. Bost, Y. Handrich, and Y. Le Maho. 2002. Buoyancy and maximal diving depth in penguins: do they control inhaling air volume? *The Journal of Experimental Biology* **205**:1189–1197.
- Schreer, J. F., K. M. Kovacs, and R. J. O. Hines. 2001. Comparative diving patterns of pinnipeds and seabirds. *Ecological Monographs* **71**:137–162.
- Skrovan, R. C., T. M. Williams, P. S. Berry, P. W. Moore, and R. W. Davis. 1999. The diving physiology of bottlenose dolphins (*Tursiops truncatus*). II. Biomechanics and changes in buoyancy at depth. *Journal of Experimental Biology* **202**:2749–2761.
- Tenney, S. M., D. Bartlett, Jr., J. P. Farber, and J. E. Remmers. 1974. Mechanics of the respiratory cycle in the green turtle (*Chelonia mydas*). *Respiration Physiology* **22**:361–368.
- van Dam, R. P., and C. E. Diez. 1996. Diving behavior of immature hawksbills (*Eretmochelys imbricata*) in a Caribbean cliff-wall habitat. *Marine Biology* **127**:171–178.
- Webb, P. M., D. E. Crocker, S. B. Blackwell, D. P. Costa, and B. J. Le Boeuf. 1998. Effects of buoyancy on the diving behavior of northern elephant seals. *Journal of Experimental Biology* **201**:2349–2358.
- Williams, T. M. 2001. Intermittent swimming by mammals: a strategy for increasing energetic efficiency during diving. *American Zoologist* **41**:166–176.
- Williams, T. M., R. W. Davis, L. A. Fuiman, J. Francis, B. L. Le Boeuf, M. Horning, J. Calambokidis, and D. A. Croll. 2000. Sink or swim: strategies for cost-efficient diving by marine mammals. *Science* **288**:133–136.
- Wilson, R. P., K. Hustler, P. G. Ryan, A. E. Burger, and E. C. Noldeke. 1992. Diving birds in cold water: do Archimedes and Boyle determine energetic costs? *American Naturalist* **140**:179–200.